THE ECOLOGY AND REPRODUCTION OF A MARINE BIVALVE, *MYSELLA PLANULATA* (ERYCINACEA)[1]

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Mysella planulata (Stimpson) is a small erycinacean bivalve which occurs primarily in muddy sands of the *Zostera marina* community. The recent distribution of *M. planulata* extends from Nova Scotia to Cape Hatteras on the American Atlantic coast and includes the Texas coast of the Gulf of Mexico. The species also occurs in Pliocene and Pleistocene deposits of Florida and Maine (Dall, 1900). While *M. planulata* is not a conspicuous member of the benthos, it may be an abundant and at times even a dominant species. Yet, as with so many other marine invertebrates of no apparent economic importance, virtually nothing is known of its biology. This report presents data on the density, distribution, growth, age-structure and reproduction of a population of *M. planulata* from Beebe Cove, at the mouth of the Mystic River, eastern Long Island Sound, Connecticut.

Beebe Cove is a small bay, approximately 1500 m long by 305 m wide. The habitat is sublittoral, but water depth does not exceed 2 m; salinity varies between 29 and 31%. The sediment is a mixture of fine sand, silt, and clays, the latter components comprising more than 70%. Beds of *Zostera marina* cover the bottom and contribute large quantities of organic detritus to the benthic ecosystem. Temperature ranges from −1 to 26° C and an ice cover may be present in winter. Beebe Cove is isolated from the Mystic River by a railroad trestle embankment and exchange occurs only through two narrow channels. Consequently, through most of the cove currents are restricted and sluggish and siltation rates are high. Except for a thin layer at the mud/water interface, the benthic environment is highly reducing.

Sampling was restricted to a single station near the center of the cove, marked with a buoy which remained in place throughout the experimental period. Most of the data in this report are based on replicate samples taken at this single station between April 1970 and November 1971, although some information is presented for the same station from sampling dates in 1969.

Replicate samples were collected using a 0.07 m² Peterson grab operated by hand from a small skiff. Samples were washed through a 1 mm mesh stainless steel screen with seawater.

For the studies on larval development, animals from the field collections were transferred to finger bowls of seawater. Frequently the act of screening and handling the adults seems to stimulate release of larvae, but a constant supply of newly released veligers was provided by adults maintained in finger bowls containing sediment from Beebe Cove. Larvae were collected every other day and

reared at a concentration of 5–20 larvae per ml, at a constant temperature of 25° C, and were fed *Isochrysis galbana* at a concentration of 100 cells/ml. Cultures were changed daily or every other day.

To determine the stage of gametogenesis, smears of live animals were prepared by removing the animals from their shells under the dissecting microscope. Soft parts were examined under a coverglass with a compound microscope, and the presence or absence of eggs, veligers and active sperm was easily determined.

Results

Density and distribution

The areal density of *Mysella* at a series of sampling dates for 1970 and 1971 is shown in Table I. The variance/mean ratio (coefficient of dispersal) is greater than unity on all dates, indicating a degree of contagion or parchiness.

TABLE I

Sampling statistics for Mysella planulata, *April 1970–November 1971 based on replicate Peterson Grab samples from a single station*

Sample No.	Date	$\bar{x}$ per Grab	S^2	Number of replicate grabs	Moment estimate of k*	1/k**
1	4/7/70	18.4	76.3	5	5.857	0.179
2	5/25	14.6	54.0	5	5.410	0.195
3	6/29	6.2	32.7	5	1.450	0.831
4	7/14	5.2	15.2	5	2.704	0.417
5	7/28	8.4	22.8	5	4.900	0.218
6	8/25	4.2	13.7	5	1.857	0.637
7	12/3	30.6	358.3	5	2.857	0.379
8	4/13/71	12.2	54.2	5	3.544	0.304
9	5/25	4.8	22.1	5	1.332	0.929
10	6/8	22.0	338.6	5	1.529	0.760
11	7/7	20.5	112.4	5	4.573	0.231
12	7/27	21.3	123.2	5	4.452	0.237
13	8/17	8.4	67.2	7	1.200	0.965
14	11/30	4.3	10.9	10	2.801	0.379

* $k = \bar{x}^2/Y'$ (see text).
** $1/k = Y'/X'$ (see text).

The negative binomial distribution is considered to be the most flexible of several mathematical frequency distributions in which the variance exceeds the mean (Anscombe, 1949; Bliss and Fisher, 1953). The parameters of this distribution are the arithmetic mean, and the exponent k. The latter is related to the spatial dispersion of organisms and its reciprocal is a measure of the degree of aggregation or clumping of the individuals in a population (Elliott, 1971). As $1/k$ approaches 0, the distribution approaches the Poisson series in which organisms are randomly distributed ($S^2 = \bar{x}$). In this study, the values of k (Table I) were calculated by the moment estimate in which $k = \bar{x}/(S^2 - \bar{x})$.

As seen in Table I, moment estimates of k ranged from 1.200 to 5.857. This would suggest a fair degree of stability over a two year period. When plotted, there does not appear to be a relationship between $\bar{x}$ and $1/k$, *i.e.*, the degree of

clumping as indicated by $(1/k)$ is not correlated with the sample mean. A rough estimate of a common k-value (k_c) has been calculated using the statistics X' and Y' where $X' = \bar{x}^2 - (S^2/n)$ and $Y' = S^2 - \bar{x}$; $1/k = Y'/X'$ (Elliott, 1971). The common k (k_c) is calculated: $1/k_c = Y'/X'$. Calculated in this way (Table I), a k_c of 2.68 is obtained.

At the single location studied, changes in density with time vary somewhat during 1971. The reasons for these differences will become clear following the discussion of age structure (see below). A feature common to both years is the decline in density which occurs during the winter and early spring. Between December 1970 and May 1971, mean density declined from 30.6 animals per grab to 4.8 per grab. After the low point in numbers is reached in late summer (Table I), no increases occur until the addition of the newly recruited year class appears
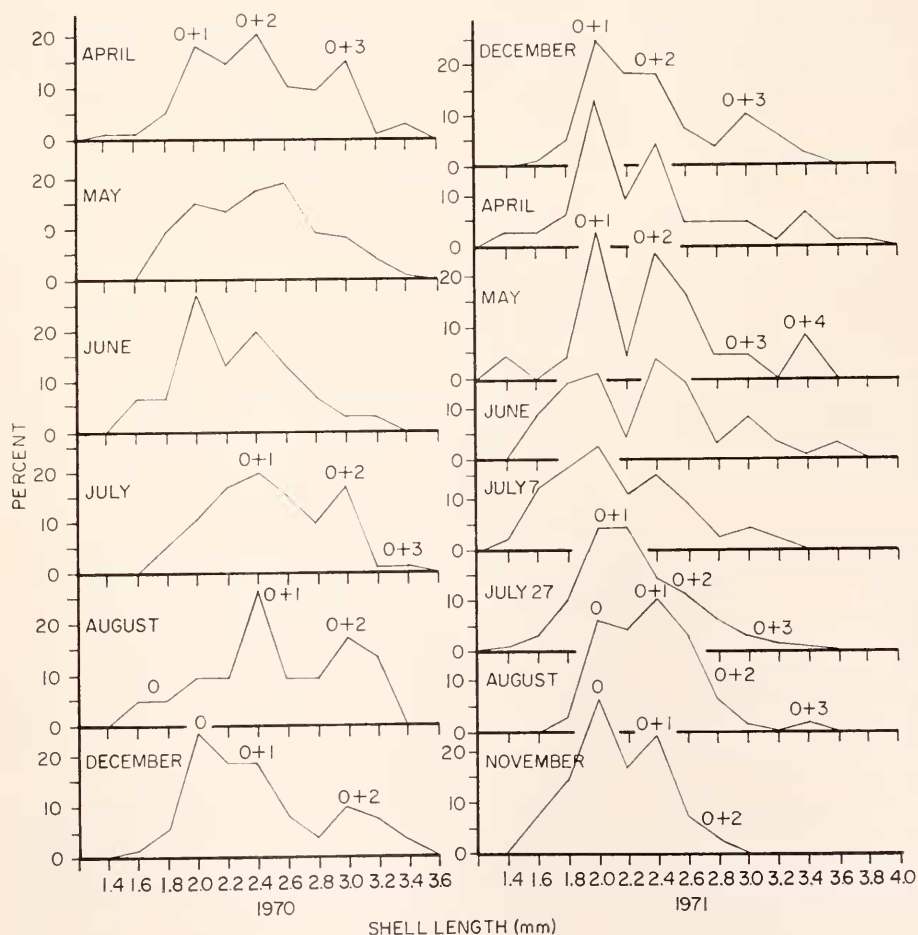

FIGURE 1. Size distribution of *Mysella planulata* populations from Beebe Cove, April 1970 through November, 1971. Numbers above the distributions indicate the age classes.

(December sample, 1970). In 1971, however, an increase in density occurred between May and June. As will be shown below, these differences are explainable on the basis of age-specific mortality, and of differences in the age composition of the population between the two years.

Population age structure and growth

Information on population age structure and size for 1970 and 1971 (Fig. 1) is supplemented by data from collections of September, 1969 (not plotted), from larval settlement collectors (Fig. 2) and from analysis of growth cessation marks (Fig. 3). The pattern revealed in the size-frequency histograms (Fig. 1) is consistent for both years. At the beginning of the growth season, the population comprises 3 fairly well-defined modal groups plus a less well-defined group at the upper end of the histogram. These peaks are considered to correspond to 3 year classes, with the remnants of possibly one or more older classes at the right. Between April and June there is an increase of very small animals in the youngest year class, particularly evident between April and May of 1970 and between May
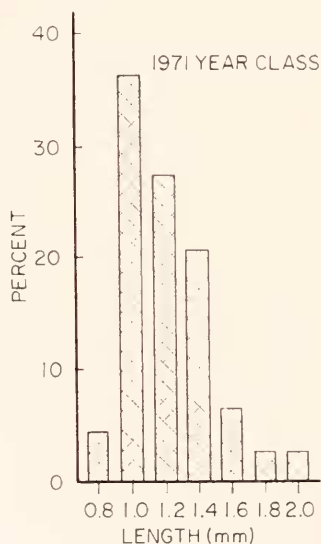

FIGURE 2. Size distribution of zero class animals from benthic collectors in Beebe Cove. This collection was retrieved on 30 August, 1971 and the animals are a maximum of 2 months old.

and June of 1971. This is accounted for by growth of very small animals which, prior to this, were below the size retained on the 1.0 mm screen. By late July, the 0 + 1 class (clams in their second growth season) is fully represented in the histograms. The new zero class makes its first appearance in August. By the end of the season, December (1970) and November (1971), the zero class is numerically dominant. The 0 + 3 class (clams in their fourth season) fades completely from the distributions by August of both years.
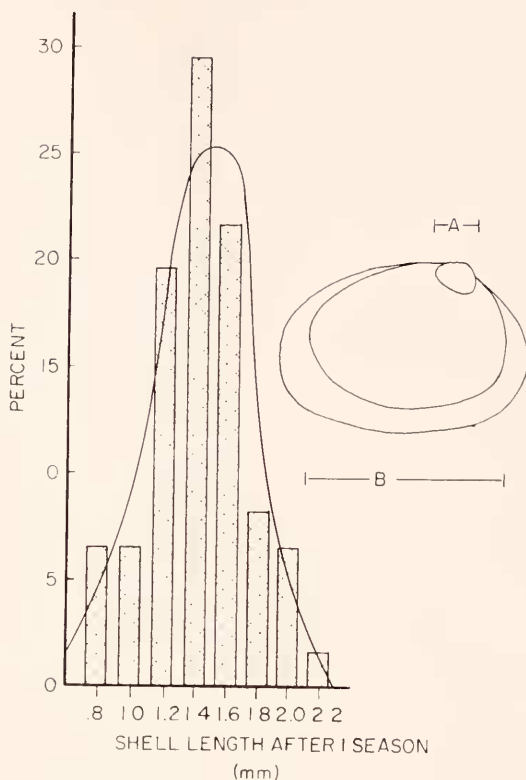
FIGURE 3. Size distribution of clams at the end of their first growing season based on length B, the maximum length at the time growth stopped. Length A represents the length of the prodissoconch (larval shell) at time of metamorphosis. The smoothed curve was fitted using normal probability paper.

The difference in density pattern between 1970 and 1971 (Table I) is largely accounted for by internal changes in the relative abundance of age groups. During both years, increments in the number of young animals occur in May and June. In 1971, this increment is reflected by the increase in density in June; in 1970, however, increases attributable to the addition of small animals were offset by mortality of older animals, the 1966 and 1967 year classes. The following year, the analogous year classes were less numerous to begin with.

Another obvious difference between the two years is evident in November 1971 where the 0 + 2 class seems to disappear completely, a trend already evident in the immediately previous sample. This is probably correlated with the drastic overall decline in the population density of *Mysella* in Beebe Cove over this period.

Figure 2 shows the length-frequency distribution of a collection of *Mysella* from Beebe Cove sediment collectors. The collectors, one-quart wide mouth glass jars (80 mm diameter) in a wood frame anchored on the bottom with several cinder blocks, were placed in the cove on 1 July and retrieved on 30 August.

Although the wooden frame rested on the bottom, the jars themselves were raised above the bottom making it unlikely that juvenile clams crawled into the collectors. The maximum age of the animals in Figure 2 is therefore 2 months. Although most of the clams in the collectors are in the 1.0 mm size class, the largest and presumably oldest have attained 2.0 mm. Figure 3 is a similar distribution of shell length (B) at the time of growth cessation. Assuming that the growth interruption mark indicates the shell length at the beginning of the new growth season (which is likely but not certain) animals range from less than 0.8 to about 2.3 mm at that time. If specimens with growth interruption marks accurately reflect the total population, the modal size at the end of the first season would be 1.4 mm (Fig. 3). This is significantly smaller than the modal size of the zero class in the size-frequency distributions for December 1970 and November 1971 in which the mode would appear to be close to 2.0 mm. However, growth cessation marks are not observable on all animals. If, for example, they are obliterated by erosion on the older animals, the distribution in Figure 3 would represent only the younger members of the zero class. While it is not possible from the present data to assign precise boundaries to the zero class, it is clear that in their first growth season these clams attain a maximum size between 2.2 and 2.5 mm with a mode between 1.4 and 2.0. By late summer (July or August) of the following year, this class attains a modal size of about 2.4 mm; and one year later, about 3.0 mm. By the end of the fourth season, the modal size may be close to 3.4 mm. While the calculations are imprecise, the overall picture is probably a reasonable approximation.

Reproductive biology

Information on gametogenesis, based on the examination of whole animal smears, is shown in Table II. In the period from April through July, active sperm were observed in almost all animals. However, developing ova were not seen until May, and the percentage of animals with developing eggs increased to a high of 67 per cent in June. By July, oogenesis had proceeded to the point where fertilized ova were seen being brooded within the mantle cavity.

The range in size of animals with sperm and ova is shown in Figure 4. Active sperm were observed in animals from 1.33 to 3.82 mm, and all individuals with developing ova were also producing active sperm. Animals with sperm but no ova ranged up to about 2.4 mm. In early spring, only individuals larger than 2.3 mm were seen to have ova, but by late May ova were seen in some smaller animals also.

TABLE II

Gametogenesis—1971

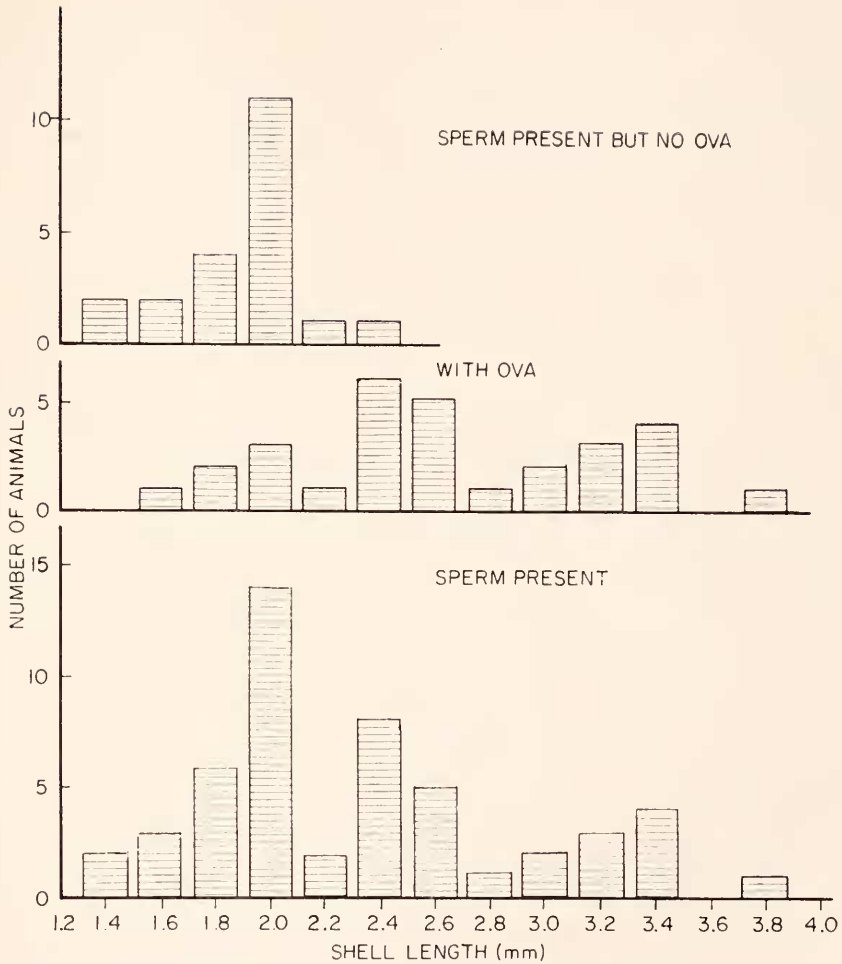| Date	No. animals examined	No. with active sperm	%	No. with ova	%
13 April	20	19	95	0	0
4 May	9	9	90	2	22
25 May	24	24	100	13	54
9 June	12	12	100	8	67
5 July	12	11	91	6	50

FIGURE 4. The relationship between gametogenesis and shell length
based on smears of living animals.

The information in Figure 4 and Table 11 shows that *Mysella planulata* is a simultaneous hermaphrodite. Spermatogenesis precedes oogenesis so that by the time the latter process begins, most of the sperm are already matured and ready for use. However, sperm are always present, even when oogenesis is maximal.

Although hermaphroditism is widespread in the Erycinacea, and occurs in all Montacutidae, the existence of self-fertilization has never been proven. In order to test this possibility in *M. planulata,* a group of 10 individuals were isolated and maintained separately in standing seawater while another group of 10 similar-sized animals was kept together to facilitate cross-fertilization. This experiment was initiated on 4 May and terminated on 23 June. During this period, the containers were undisturbed and the water was not changed. At the end of the experimental

period, veliger larvae were observed in the grouped control. But four of the ten isolated animals had also produced veliger larvae. Since the animals were isolated before ova had matured and entered the suprabranchial cavity, the fertilization of the ova leading to the release of the veligers by the isolated specimens must have been effected by self-fertilization. This experiment does not eliminate the possibility that cross-fertilization may also occur. It is significant, however, that no spontaneous release of sperm has ever been observed.
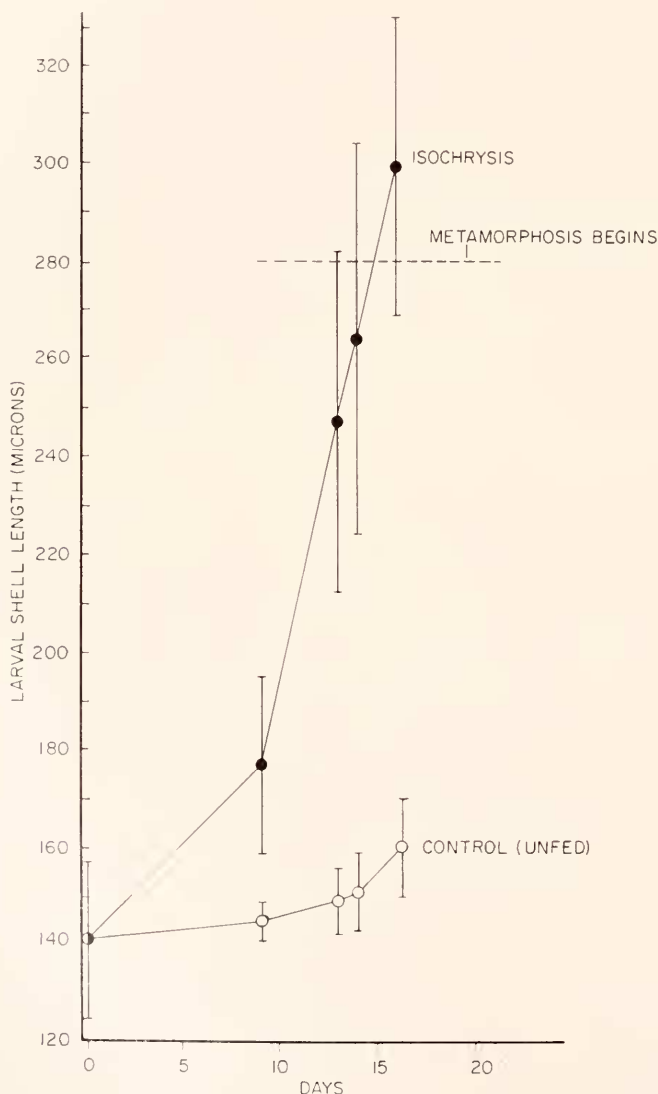

FIGURE 5. Cumulative growth curves of *Mysella* larvae reared in the laboratory. Solid circles, fed *Isochrysis galbana;* clear circles, starved. Lines indicate standard errors of the means. The horizontal dashed line shows the approximate size at which metamorphosis begins.

Development

Fertilized ova in cleavage stages were observed in the suprabranchial cavity toward the end of May. By early June, development had proceeded to the veliger stage. Most veligers appear to be released in June but a small proportion of animals continued to release larvae into July or even August. At emergence, the veliger shell length ranged from 126 to 150 microns ($\bar{x} = 141 \pm 16$ microns) and larvae are at the straight-hinge stage. A cumulative growth curve for larvae reared in the laboratory is shown in Figure 5. Although there is significant growth in the starved control group, these never exceed 160 microns and do not metamorphose. It is clear that the larvae of *M. planulata* are planktotrophic: the veligers must feed on the plankton and grow in order for metamorphosis to occur. Variability in size of the fed larvae is high. Some individuals grow rapidly, others very slowly. Metamorphosis begins in cultures at about 15 days and pediveligers, at metamorphosis, range from 225 to 355 microns.

Figure 6 shows the prodissoconch length-frequency distribution for a series of laboratory grown animals as compared with field-collected juveniles. The means of 299 and 286 microns (laboratory-reared and field-collected specimens, respectively) are not significantly different. However, the variance of the field-collected population is significantly lower than the variance of the laboratory-reared group.
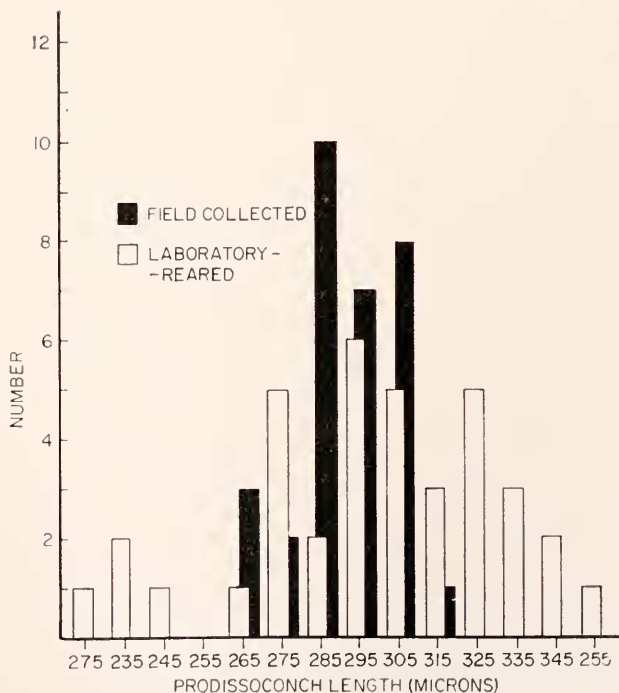

FIGURE 6. Prodissoconch length-frequency distributions for laboratory-reared and field-collected *Mysella*.

DISCUSSION

It is evident from Table I that *Mysella planulata* exhibits a fairly constant high degree of clumping. Values of k in the same range ($0 < k < 5$) were reported by Lie (1968) for the related species *Mysella tumida* in Puget Sound. Lie suggested that the high degree of patchiness shown by *M. tumida* is correlated with brood protection. However, the present study shows that although larvae are retained for a period of time, they nevertheless spend a significant period of time in the plankton and are therefore not restricted to settling in close proximity to adult parent clams.

Possibly late stage larvae are attracted by the presence of adults in the substrate, resulting in a non-random distribution. Alternately, a gregarious response may occur following metamorphosis. In view of the capacity of *Mysella* for self-fertilization, gregariousness would have the beneficial effect of increasing heterozygosity in the gene pools of local aggregations.

A high degree of contagion might be expected in symbiotic species, which include many—perhaps the majority—of erycinacean bivalves, assuming that the host species are themselves contagiously distributed. However, this study provides no evidence for an obligative symbiosis with any invertebrate species, and even a facultative or temporary symbiosis seems unlikely. Small specimens and dead shells are sometimes found adhering to the podia of *Thyone briareus,* a burrowing holothurian. But this is of doubtful significance because the podia of *Thyone* tend to adhere to a variety of detritus. In any case, *M. planulata* gives every indication of being free-living in Beebe Cove, where it lives in the upper oxygenated layer of sediment. Full understanding of its distribution may require a better knowledge of how *Mysella* functions in this microhabitat. The eel grass itself is not distributed evenly over the bottom. Even within a dense *Zostera* stand, patches of bare or almost bare substrate occur. The microenvironment within a *Zostera* meadow has not been studied but it is possible that this is the key to the non-random distribution of *M. planulata*.

In common with other Erycinacea, *Mysella planulata*, exhibits larviparity (the mode of development in which the eggs develop within the confines of the maternal body and are then released as larvae) and partial brood protection. *M. planulata* is also a simultaneous hermaphrodite. As noted by Fretter and Graham (1964), simultaneous hermaphroditism in marine bivalves appears to be linked with brood protection, particularly in the form of ovoviviparity and viviparity. These forms of brood protection, whatever their specific selective advantage, reinforce non-random dispersal since juveniles occur in close proximity to their parents. The loss of a larval dispersal phase may be compensated by the advantage of access to a suitable substrate immediately upon release from the female, particularly in bivalves of restricted habitats. Sellmer (1967) noted that brood protection is most prevalent among very small bivalves and may be related to the efficiency of egg production. Very small animals may simply lack the energy resources to produce enough planktotrophic eggs to guarantee survival. The larviparity of *Mysella planulata* confers the benefits of both brood protection and planktonic larvae. Retention of the early larval stage provides protection during a critical period but the subsequent release of planktotrophic veligers allows the species to

exploit the phytoplanktonic food source as well as providing a mechanism of dispersal.

Mysella varies seasonally in abundance. Jørgensen (1946) observed that the larvae of *M. bidentata* constitute an important part of the plankton of the Øresund at certain times of the year. In the Beebe Cove benthos, population densities exceeding 5000 per m² have been observed in late summer and fall, mostly newly-settled juveniles. At other times, populations of adults rarely exceed 600 per m² in this area, and may be much less. Thus, such a diminutive and inconspicuous species may assume an unexpectedly significant part in the function of this ecosystem by virtue of its role as a secondary producer in the plankton, and the subsequent transfer of energy into the benthos where it is available for exploitation by upper trophic levels of the benthic food chain.

In Beebe Cove, larvae metamorphose at a size between 265 and 315 microns with a mean of 299 microns. The greater range among laboratory-reared individuals suggests that in nature environmental factors—most likely predation—eliminate individuals which either delay metamorphosis or develop too slowly.

The data presented above show that *Mysella planulata* is a small (<4.0 mm) bivalve, a simultaneous hermaphrodite with larviparous development. For most individuals sexual maturity occurs in the third season. Mature animals produce up to 1000 eggs per season. Fertilized eggs are retained in the suprabranchial chamber until the larvae attain the straight-hinge stage and are released as planktotrophic veligers. Larvae settle after about two weeks in the plankton (Fig. 5). Animals continue to grow and reproduce and live a maximum of about 4 years.

The picture which emerges is of a species which, despite its minute size, exhibits a degree of iteroparity, *i.e.*, the capacity to reproduce at least twice per lifetime. The significance of this is apparent when considered in the light of the fecundity of the species. Since egg production is limited to animals larger than 1.7 mm, probably not more than 25 per cent of the 0 + 1 class contributes to the annual egg production. Estimates of the potential reproductive contribution of the various age classes in the population at the beginning of the reproductive season are shown in Figure 8. The estimates were made with the aid of the regression (Fig. 7), relating total eggs produced as a function of shell length. The numbers of individuals attributable to the several age classes were determined by visually assigning limits to the modal size groups. The potential egg production for each size class was calculated by multiplying the numbers of individuals in that class by the total number of larvae released per adult (Fig. 7). The production of all the size classes within each age class was summed and the proportion of the total egg production attribute to each age class determined (Fig. 8). Where age class limits overlap, potential egg production was divided evenly between adjacent classes.

The estimates assume that only a single batch of larvae is released per adult clam. It is possible that a second brood of fertilized eggs passes into the suprabranchial chamber of the clams following the release of the initial batch of veligers. However, dissections of brooding animals indicate very few maturing ova retained in the ovaries. The scatter in Figure 7 probably arises from abnormally low counts which could be explained by the occurrence of secondary broods. In any case, it is probable that the regression in Figure 7 under estimates egg production
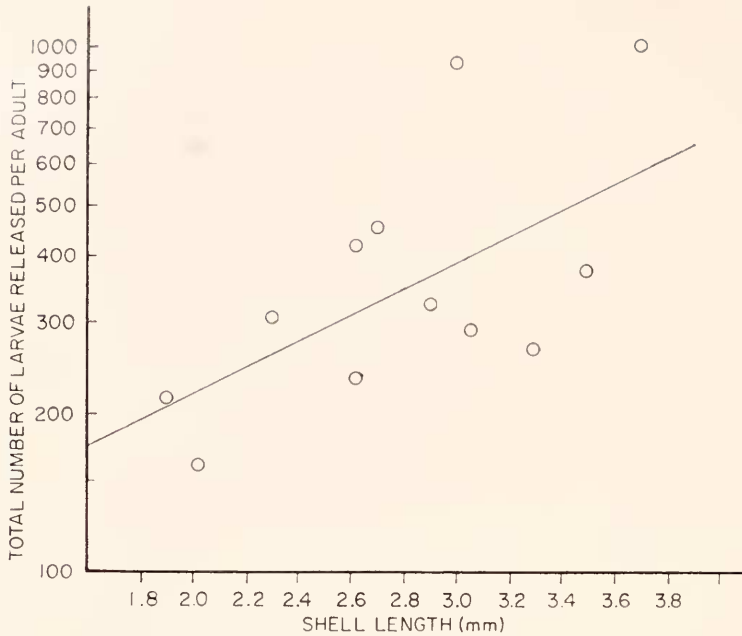
FIGURE 7. Relationship between shell length and the total number of larvae released per adult. The regression line is fitted by the method of least squares: $Log_{10}Y = 1.860 + 0.243X$ where X is shell length and Y is the number of larvae.
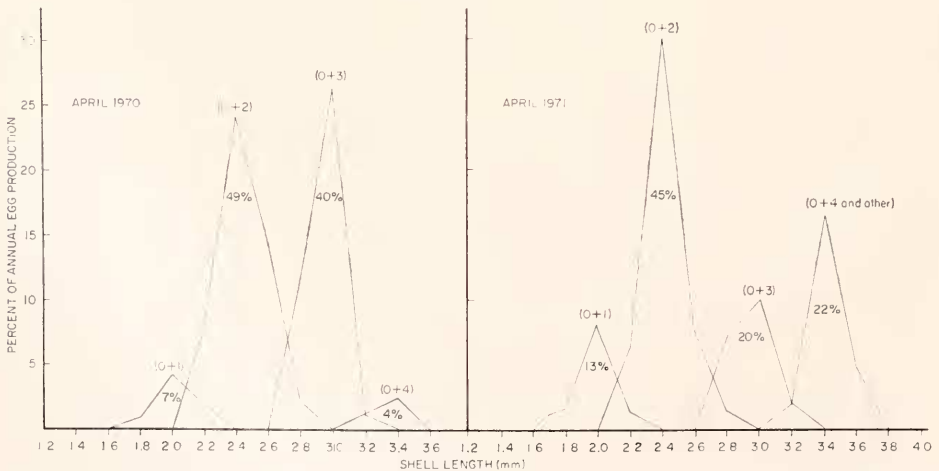

FIGURE 8. Potential reproductive contribution of age classes at the beginning of the reproductive seasons, April 1970 and 1971. Numbers in parenthesis above the distributions indicate the age classes; numbers under the peaks indicate the percentage contribution of the age groups.

of the larger individuals and probably overestimates production by very small individuals.

It is evident from Figure 8 that although the major reproductive burden is carried by the $0 + 2$ class (clams in their 3rd growing season), the remaining year classes, and particularly the older classes, do contribute significantly to the annual production. This pattern is adaptive since it provides a margin of safety against the loss of one or more entire year classes. Between 1970 and 1971, (Fig. 8) the potential reproductive contribution of the $0 + 3$ class dropped from about 40% in 1970 to 20% in 1971. This was caused by high mortality in the 1968 year class, which is the $0 + 2$ class in 1970 and becomes the $0 + 3$ class in 1971.

Murphy (1968) provides evidence that iteroparity has selective advantages in species in which there is uncertainty in survival from zygote to first maturity. In the case of *Mysella*, as with other planktotrophic temperate species, variability in the survival of the zero class is normal. This variability may result from variation in the level of predation pressure on larvae and juveniles, and in density-independent environmental factors such as unfavorable currents, unusually severe reducing conditions in the sediment, *etc*. Where environmental instability may cause fluctuations in population density, the adaptive value of distributing the reproductive responsibility over a wider range of age groups is obvious. The $0 + 2$ class, which evidently bears the major reproductive burden, represents the best possible compromise between maximum numbers of individuals and maximum biomass per individual.

Iteroparity is not the only reproductive option open to small marine bivalves. The venerid clam *Gemma gemma* is an ovoviviparous species which appears to reproduce only once (Sellmer, 1967; Green and Hobson, 1970). Populations of *Gemma* are known to suffer severe predation so that there may be an adaptive advantage for this species to mature and reproduce rapidly. Ovoviviparity in *Gemma* could be interpreted primiarily as a mechanism for enhancing survival of offspring, thus increasing biotic potential. In *Mysella*, however, the occurrence of a planktonic dispersal phase puts a constraint on the development toward complete brood protection. The adjustment toward iteroparity may thus be interpreted as an alternate option for increasing biotic potential.

The feeding mechanism of *M. planulata* was not studied. However, from the posture of the living animal *in situ*, and its normal location at the sediment/water interface, either detrital organic matter or suspended material is potentially available for food. Unlike the situation in most bivalves, except the Protobranchia and certain primitive eulamellibranch genera, the pathway of water through the mantle cavity of *Mysella* and related genera is anterior to posterior. There are no siphons; gill filaments are few in number and, in *M. planulata*, the outer demibranchs are reduced in size. Ciliary currents are present but weak. The palps are also quite small but their appressed surfaces are grooved and ciliated, suggesting the presence of a sorting mechanism. A distal food groove is present on the ctenidia. All of these morphological characters suggest suspension feeding. The suspended matter is quite likely very small aggregates of particulate organic matter, some or all of which may be resuspended by the movement of the animal as it moves through the sediment. Nevertheless, a role for dissolved organic material in this species is not ruled out.

SUMMARY

1. In Beebe Cove, a shallow sublittoral bay, the bivalve *Mysella planulata* is dispersed contagiously throughout the year. This dispersion is not associated with the mode of development of the species but may be correlated with non-random variability in the microhabitat. There is no evidence that *M. planulata* in Beebe Cove is symbiotically associated with any invertebrate species.

2. *Mysella planulata* has a life span encompassing four growing seasons and a maximum size of about 4.0 mm. About 50% of maximum length is attained by the end of the first growing season.

3. *Mysella planulata* is a simultaneous hermaphrodite. Spermatogenesis precedes oogenesis. The species is capable of self-fertilization and although no animals were ever observed to release sperm, the possibility of cross-fertilization is not ruled out. Egg production is limited to animals in excess of 1.7 mm.

4. Larvae are retained in the suprabranchial chamber to the straight-hinge stage of development. Upon release, the larvae are planktotrophic; starved larvae in culture grow slightly but will not metamorphose. Metamorphosis in culture occurs in about two weeks at 25° C. In the laboratory, larvae metamorphose over a wider range of size than in nature, probably reflecting predation pressure in nature.

5. Estimates of the potential reproductive contribution of the various age classes show that although the major burden is carried by animals in their 3rd season (0 + 2 class), older classes contribute significantly. This pattern is adaptive in unstable environments where high mortality of the 0-year class is probable.

6. On morphological grounds, *M. planulata* is believed to be a suspension feeder; probably feeding on very fine particulate organic matter.

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